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LIFE SCIENCES DIVISION

GRANT TITLE: The Fossil Record of Evolution: Data on Diversification and Extinction

GRANT NUMBER: NAG 2-282

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INTRODUCTION

NASA Grant NAG 2-282, entitled "The Fossil Record of Evolution: Data on Diversification and Extinction" supported two principal efforts:

1. Compilation of a synoptic, mesoscale data base on times of origination and extinction of animal genera in the oceans over the last 600 million years (myr) of geologic time;

2. Analysis of statistical patterns in these data that relate to the diversification of complex life and to the occurrence of mass extinctions, especially those that might be associated with extraterrestrial phenomena.

The data base is unique in its taxonomic scope and detail and in its temporal resolution. It has proved to be a valuable resource for investigating evolutionary expansions and extinctions of complex life by the principal investigator and collaborators.

BACKGROUND

The project was proposed in the wake of two important discoveries in the early 1980's:

1. Geochemical anomalies at the Cretaceous-Tertiary Boundary that implicated impact of a large asteroid or comet in the extinction of dinosaurs and other organisms at the end of the Cretaceous Period (Alvarez et al. 1980);

2. A 26-myr periodicity of extinction events, which included the Cretaceous-Tertiary mass extinction and thus implicated impacts as causes of other extinctions (Raup and Sepkoski 1984).

At the time of these publications, there was only a crude phenomenology of mass extinction involving identity of events, comparison of magnitudes and durations, documentation of taxonomic, ecologic, and geographic selectivity, and contrast with intervening times of "background" extinction. Much of the comparative work had been done with data on taxonomic families (about 3500 in all) at the stage-level of temporal resolution (about 7.5 myr long on average). These data, while adequate for answering some questions, suffered from

1. the small sample size, which prevented detailed analysis of the differential response of various taxa to mass extinction;

2. the damping effect of families, which normally contain many species and thus are insensitive to smaller extinction events, making their identification difficult;

3. the averaging aspect of long stratigraphic stages, which blurs the distinction between short-term extinction events and longer-term background intervals within single stages.

These problems were recognized in the NASA report on the Evolution of Complex and Higher Organisms (ECHO: Milne et al. 1985), which recommended assembly of more detailed compendia of fossil data on occurrences and distributions of complex animals and plants.

Based on my experience compiling familial data (Sepkoski 1982), I proposed a new, more detailed data base assembled at

1. the genus level, a taxonomic rank closer to the actual unit of evolution (i.e., species) with approximately 10 times more named taxa than families;

2. the substage level, an international stratigraphic interval averaging 3.6 myr in duration, about half that of previous data bases (Fig. 1).

It was proposed to restrict this compilation to marine animals since the oceans represent a discrete evolutionary arena with a fossil record that is more complete and more extensively studied than its counterpart for terrestrial ecosystems.

NASA was an appropriate agency from which to seek support since the project's aims related to several areas of interest, including the following:

1. The role of extraterrestrial phenomena in biotic extinction, especially in relation to

   a. understanding the biotic effects of the Cretaceous-Tertiary event and subsequent restructuring of global marine faunas;

   b. testing the hypothesis of a 26-myr periodicity in extinction, which has implications for space research;

   c. generating a "road map" of extinction events that could be explored in the geologic record for evidences of other bolide impacts (cf. McLaren 1983);

2. The habitability of the Earth, especially with regards to the sensitivity of the biota to perturbations of various kinds and magnitudes and to the histories and time scales of biotic recovery;

3. The details of the megaevolutionary history of complex life on Earth and its potential relevance to the development of intelligent life elsewhere in the Universe.

RECENT	R
QUATERNARY	Q
Pleistocene	Q (Plei)
TERTIARY	T
Pliocene	T (Plio)
Miocene	T (Mi)
Upper Miocene	T (Mi-u)
Messinian	T (Mi-u-u)
Tortonian	T (Mi-u-l)
Middle Miocene	T (Mi-m)
Lower Miocene	T (Mi-l)
Burdigalian	T (Mi-l-u)
Aquitanian	T (Mi-l-l)
Oligocene	T (Ol)
Upper Oligocene	T (Ol-u)
Lower Oligocene	T (Ol-l)
Eocene	T (Eo)
Upper Eocene	T (Eo-u)
Middle Eocene	T (Eo-m)
Bartonian	T (Eo-m-u)
Lutetian	T (Eo-m-l)
Lower Eocene	T (Eo-l)
Paleocene	T (Pale)
Thanetian	T (Than)
Danian	T (Dani)
CRETACEOUS	K
Upper Cretaceous	K (u)
Senonian	K (Sn)
Maestrichtian	K (Maes)
upper	K (Maes-u)
lower	K (Maes-l)
Campanian	K (Camp)
upper	K (Camp-u)
lower	K (Camp-l)
Santonian	K (Sant)
upper	K (Sant-u)
lower	K (Sant-l)
Coniacian	K (Coni)
upper	K (Coni-u)
lower	K (Coni-l)
"middle" Cretaceous	K (m)
Turonian	K (Turo)
upper	K (Turo-u)
lower	K (Turo-l)
Cenomanian	K (Ceno)
upper	K (Ceno-u)
middle	K (Ceno-m)
lower	K (Ceno-l)
Lower Cretaceous	K (l)
Albian	K (Albi)
upper	K (Albi-u)
middle	K (Albi-m)
lower	K (Albi-l)
Aptian	K (Apti)
upper	K (Apti-u)
lower	K (Apti-l)
Barremian	K (Barr)
upper	K (Barr-u)
lower	K (Barr-l)
Neocomian	K (Nc)
Hauterivian	K (Haut)
upper	K (Haut-u)
lower	K (Haut-l)
Valanginian	K (Vala)
upper	K (Vala-u)
lower	K (Vala-l)
Berriasian	K (Berr)
upper	K (Berr-u)
lower	K (Berr-l)
JURASSIC	J
Upper Jurassic	J (u)
Tithonian	J (Tith)
upper	J (Tith-u)
lower	J (Tith-l)
Kimmeridgian	J (Kimm)
upper	J (Kimm-u)
lower	J (Kimm-l)
Oxfordian	J (Oxfo)
upper	J (Oxfo-u)
middle	J (Oxfo-m)
lower	J (Oxfo-l)
Middle Jurassic	J (m)
Callovian	J (Call)
upper	J (Call-u)
middle	J (Call-m)
lower	J (Call-l)
Bathonian	J (Bath)
upper	J (Bath-u)
middle	J (Bath-m)
lower	J (Bath-l)
Bajocian	J (Bajo)
upper	J (Bajo-u)
lower	J (Bajo-l)
Aalenian	J (Aale)
Lower Jurassic	J (l)
Toarcian	J (Toar)
upper	J (Toar-u)
lower	J (Toar-l)
Pliensbachian	J (Plie)
upper	J (Plie-u)
lower	J (Plie-l)
Sinemurian	J (Sine)
upper	J (Sine-u)
lower	J (Sine-l)
Hettangian	J (Hett)
upper	J (Hett-u)
lower	J (Hett-l)
TRIASSIC	Tr
Upper Triassic	Tr (u)
Norian	Tr (Nori)
Rhaetian	Tr (Rhae)
upper	Tr (Nori-u)
middle	Tr (Nori-m)
lower	Tr (Nori-l)
Carnian	Tr (Carn)
upper	Tr (Carn-u)
lower	Tr (Carn-l)
Middle Triassic	Tr (m)
Ladinian	Tr (Ladi)
upper	Tr (Ladi-u)
lower	Tr (Ladi-l)
Anisian	Tr (Anis)
upper	Tr (Anis-u)
middle	Tr (Anis-m)
lower	Tr (Anis-l)
Lower Triassic	Tr (l)
Olenekian	Tr (Olen)
Spathian	Tr (Olen-u)
Smithian	Tr (Olen-l)
"Nammalian"	Tr (Nm)
Induan	Tr (Indu)
Dienerian	Tr (Indu-u)
Griesbachian	Tr (Indu-l)
PERMIAN	P
Upper Permian	P (u)
Tartarian	P (Tatr)
Dorashamian	P (Dora)
Djhulfian	P (Djhu)
"middle" Permian	P (m)
Guadalupian	P (Guad)
upper	P (Guad-u)
lower	P (Guad-l)
Lower Permian	P (l)
Leonardian	P (Leon)
upper	P (Leon-u)
middle	P (Leon-m)
lower	P (Leon-l)
Wolfcampian	P (Wc)
Sakmarian	P (Sakm)
upper	P (Sakm-u)
lower	P (Sakm-l)
Asselian	P (Asse)
upper	P (Asse-u)
lower	P (Asse-l)
CARBONIFEROUS	C
Upper Carboniferous	C (u)
Pennsylvanian	C (Pn)
Stephanian	C (Step)
Gzelian	C (Step-u)
Kasimovian	C (Step-l)
Moscovian	C (Mosc)
upper	C (Mosc-u)
lower	C (Mosc-l)
Bashkirian	C (Bash)
upper	C (Bash-u)
lower	C (Bash-l)
Mississippian	C (Ms)
Serpukhovian	C (Serp)
upper	C (Serp-u)
lower	C (Serp-l)
Lower Carboniferous	C (l)
Visean	C (Vise)
upper	C (Vise-u)
lower	C (Vise-l)
Tournaisian	C (Tour)
upper	C (Tour-u)
lower	C (Tour-l)
DEVONIAN	D
Upper Devonian	D (u)
Famennian	D (Fame)
upper	D (Fame-u)
middle	D (Fame-m)
lower	D (Fame-l)
Frasnian	D (Fras)
upper	D (Fras-u)
middle	D (Fras-m)
lower	D (Fras-l)
Middle Devonian	D (m)
Givetian	D (Give)
upper	D (Give-u)
lower	D (Give-l)
Eifelian	D (Eife)
upper	D (Eife-u)
lower	D (Eife-l)
Lower Devonian	D (m)
Emsian	D (Emsi)
upper	D (Emsi-u)
lower	D (Emsi-l)
Siegenian	D (Sieg)
upper	D (Sieg-u)
lower	D (Sieg-l)
Gedinnian	D (Gedi)
upper	D (Gedi-u)
lower	D (Gedi-l)
SILURIAN	S
Upper Silurian	S (u)
Pridolian	S (Prid)
Ludlowian	S (Ludl)
upper	S (Ludl-u)
lower	S (Ludl-l)
Wenlockian	S (Wenl)
upper	S (Wenl-u)
lower	S (Wenl-l)
Llandoverian	S (Ldov)
upper	S (Ldov-u)
middle	S (Ldov-m)
lower	S (Ldov-l)
ORDOVICIAN	O
Upper Ordovician	O (u)
Ashgillian	O (Ashg)
Hirnantian	O (Ashg-u)
middle	O (Ashg-m)
Pusgillian	O (Ashg-l)
Middle Ordovician	O (m)
Caradocian	O (Cara)
upper	O (Cara-u)
middle	O (Cara-m)
lower	O (Cara-l)
Llandeilan	O (Llde)
upper	O (Llde-u)
lower	O (Llde-l)
Llanvirnian	O (Llvi)
upper	O (Llvi-u)
lower	O (Llvi-l)
Lower Ordovician	O (l)
Arenigian	O (Aren)
upper	O (Aren-u)
lower	O (Aren-l)
Tremadocian	O (Trem)
upper	O (Trem-u)
lower	O (Trem-l)
CAMBRIAN	Cm
Upper Cambrian	Cm (u)
Trempealeauan	Cm (Trep)
upper	Cm (Trep-u)
lower	Cm (Trep-l)
Franconian	Cm (Fran)
upper	Cm (Fran-u)
lower	Cm (Fran-l)
Dresbachian	Cm (Dres)
upper	Cm (Dres-u)
lower	Cm (Dres-l)
Middle Cambrian	Cm (m)
upper Middle	Cm (uMid)
upper	Cm (uMid-u)
middle	Cm (uMid-m)
lower	Cm (uMid-l)
mid Middle	Cm (mMid)
upper	Cm (mMid-u)
lower	Cm (mMid-l)
lower Middle	Cm (lMid)
upper	Cm (lMid-u)
lower	Cm (lMid-l)
Lower Cambrian	Cm (l)
Botomian	Cm (Boto)
upper	Cm (Boto-u)
lower	Cm (Boto-l)
Atdabanian	Cm (Atda)
upper	Cm (Atda-u)
lower	Cm (Atda-l)
Tommotian	Cm (Tomm)
upper	Cm (Tomm-u)
lower	Cm (Tomm-l)
VENDIAN	V
Nemakit-Daldyn	V (N-Da)
Upper Vendian	V (u)

Figure 1. Stratigraphic units and codes used for time intervals of origination and extinction in the genus-level data base. Geologic systems have a one- or two-letter code. This is followed in parentheses by a code for subinterval if known: one or tewo letters for series, four letters for stage, and one letter preceded by a hyphen for substage. Note that there are nearly twice as many substage intervals as stages.

ORIGINAL PAGE IS OF POOR QUALITY

METHODOLOGY

The methodology employed in the funded project was initially a straightforward (although more time consuming) expansion of approaches used to compile familial data. All steps involved extensive surveys of the international paleontologic literature, executed mostly by the principal investigator but aided by graduate assistants supported by grant funds. The steps involved are outlined below:

1. A preliminary data base was assembled by transcribing information from older paleontologic syntheses, principally the Treatise on Invertebrate Paleontology (Moore et al. 1953-1984) and Vertebrate Paleontology (Romer 1966). These data, taken only for marine animal genera, were immediately entered into computer files.

2. The preliminary data were augmented by adding newly discovered genera and enhancing rather crude temporal data with such major secondary sources as Osnovy Paleontologii (Orlov 1958-1964), The Fossil Record (Harland et al. 1967), Handbook of Paleoichthyology (Schultze 1978-1987), and Encyclopedia of Paleoherpetology (Wellnhofer 1969-1981).

3. Finally, updated taxonomy, new genera, taxonomic synonymies, and more highly resolved times of first and last occurrences of genera were obtained from another approximately 900 journal articles, monographs, and secondary sources. This activity involved

   a. perusing all new paleontologic literature arriving in the science library of the University of Chicago;

   b. tracking down specific references for relevant data;

   c systematically surveying complete journal series from 1970 to date, including Acta Palaeontologica Polonica (Poland), Alcheringa (Australia), Annales de Palèontolgies (Invertebrès) (France), Bulletins of American Paleontology (USA), Journal of Paleontology (USA), Micropaleontology (USA), Palaeontographica Polonica (Poland), Paläontologische Zeitschrift (FDR), Paleontological Journal (USSR), and Palaeontology (UK).

Additionally, several paleontologists kindly shared unpublished data bases for several taxonomic groups, including Carboniferous to Triassic gastropods (D. Erwin), North American Ordovician trilobites (R. Sloan), Phanerozoic brachiopods (R. Cowen), and Cambrian problematica (S. Bengtson).

My ability to obtain high-resolution global data on times of origination and extinction of genera was made possible by ongoing international efforts to define the geologic time scale more precisely and to correlate intervals around the world. These are efforts of the International Union of Geological Sciences (IUGS)

Commission on Stratigraphy and of the International Geological Correlation Projects (IGCP). Many of the results of these projects were summarized in Harland et al. (1982, 1989), the first of which was used extensively, although with numerous corrections and emmendations.

RESULTS

A preliminary, computerized data base was assembled during the first 15 months of the project. Included were data on marine animal-like protists, invertebrates, and vertebrates. The structure chosen to store data was simply designed to permit rapid compilation and editing of data (both visually and electronically); it also permited rapid computations of diversity and evolutionary rates. As illustrated in Fig. 2, each fossil genus is given one line of ASCII code with the following information:

1. genus name;
2. hierarchical code for stratigraphic interval of first known occurrence in the fossil record (Fig. 1);
3. code for last known occurrence;
4. numerical code for literature source(s) of information, where appropriate.

The preliminary data assembled in 1984 encompassed somewhere between one-half and two-thirds of known marine animal genera. In subsequent years, the data base was expanded and the temporal resolution enhanced. The table below provides an index of progress that was made.

Stratigraphic Resolution	Average Duration	1984 #	1984 %	1985 #	1985 %
Substage	3.6 myr	6204	33%	13720	51%
Stage	7.3 myr	6901	37%	8011	30%
Series	19.7 myr	4105	22%	4306	16%
System	57.0 myr	1562	8%	675	3%
Total:		18772		26712	

This table lists the number of extinct genera in the data base near the beginning and end of the project. Lines give numbers of genera with times of extinction resolved to each of the four levels in the stratigraphic hierarchy of geologic time: systems (e.g., Cretaceous), series (e.g., Upper Cretaceous), stages (e.g., Maastrichtian), and substages (e.g., upper Maastrichtian). In the preliminary data base of 1984, 1562, or 8% of the total

Cl. BIVALVIA (Classification and basic stratigraphic data from the Treatise, Pt. N [1969]).

Or. NUCULOIDA

Acila	T (Ol)	- R *	
Adrana	T (Eo-m-1)	- R	(700)
+Afganodesma	O (1)		(98)
Arisaigia	S (Wenl-1)		
+Australoneilo	T (Eo-u)		
+Australoportlandia	T (Eo-u)		
Bicrenula	D (Fras)		
Borissia	T (Mi)?		
Brevinucula	T (Mi)	- R	
Cadomia	O (Llde-u)		
Calorhadia	T (Eo-1)	- T (Eo-u)	(700)
Cardiolaria	O (Llde)	- S (Ludl)	
Clinopista	D (Gedi)	- P (Sakm)	
+Cnesterium	T (Mi)	- R *	(816)
Concavodonta	O (Cara-u)	- O (Ashg-m)	
Costatoleda	T (Ol)	- R	
Ctenodonta	O (Aren-u)	- O (Ashg-m)	(91)
Ctenodontella	D (1)		
+Dacryomya	Tr(1)	- J (Tith)	(159)
Deceptrix	O (Llvi-1)	- D (1)	(91)
Ditichia	D (1)		
Dysondonta	D (Emsi)?		
+Economolopsis	C (Serp-1)		(879)
Ekstadia	S (Wenl-u)		(95)
+Ennucula	T (Eo-u)	- R	(530)
Ezonuculana	K (Coni)?	- K (Maes)	(159)
Gibbonucula	T (Eo-1)		
Glyptoleda	P (Guad-1)		(745)
+Gotodonta	S (Ldov-u)	- D (Give)	(97)
Hataiyoldia	T (Mi)		
Hilgardia	T (Eo-m-u)		(700)
+Indoculana	J (Call-1)		
Isoarca	J (Aale)	- K (Sn)	(92)
Jupiteria	K (Albi)?	- R	(789)
Kalayoldia	T (Eo-u)	- R *	(816)
Koenenia	D (1)		
Lamellinucula	T (Eo-m-u)	- R *	(700)
Ledella	T (Eo-u)	- R	(530)
Ledina	T (Dani)	- T (Eo-u)	(700)
Ledopsis	D (1)		
Leionucula	K (Haut-1)	- R	(789)
Lembulus	T (Eo)	- R	
Linucula	T (Mi-m)	- R	(681)
Lithorhadia	T (Dani)	- T (Mi-m)	(816)
Malletia	K (Vala-1)	- R *	
Megayoldia	T (Ol)	- R *	(816)

Figure 2. A sample portion from one of the 29 files in the genus-level data base. Below introductory text, genera are listed alphabetically within each taxonomic order; "+" before a name signifies a genus not listed in the preliminary data source (in this case, the Treatise on Invertebrate Paleontology). After each name are two sets of alphanumeric codes for stratigraphic intervals of first and last known occurrence in the fossil record (see Fig. 1); a single code set indicates that the genus is known from only one interval. A "*" following an "R" (for Recent) indicates that an extant genus is also known from fossils in the Pliocene and/or Pleistocene. The numbers in parentheses in the final column are codes for the literature source(s) of the stratigraphic and/or taxonomic information, if different from the basic source.

number of extinct genera, had times of extinction resolved to the unexceptably coarse level of systems, which average 57 myr long. Five years later, this number had been reduced to 675, or 3% of extinct genera. During the same interval, nearly 8,000 extinct genera were added to the data base, increasing its size by approximately 40%. (The total size of the data base, including genera extant in the modern oceans, grew to over 31,000 names.) Most of the genera that were added had high-resolution times of origination and extinction. This, combined with continuous gathering of higher quality data on genera already in the data base, increased the average temporal resolution from about 12.9 myr in 1984 to 8.7 myr in 1989, a 46% improvement relative to the theoretical mesoscale limit of 3.6 myr.

In addition to compiling and editing data, various bookkeeping and graphics computer programs were developed. These dedicated programs permitted rapid computation of diversity statistics and evolutionary rates for parts or all of the data base. They also provided rapid graphical display of these numbers as functions of geologic time. All aided immensely in the published investigations described below.

COMPLETED PROJECTS

The following papers and abstracts were published with support from NASA grant NAG 2-282. They involve either direct analyses of the evolving data base or essays dependent on insights gained from working with the data.

Papers:

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3. D.M. Raup and J.J. Sepkoski, Jr. 1986. Periodic extinction of families and genera. Science 231:833-836.

4. J.J. Sepkoski, Jr. and D.M. Raup. 1986. Was there 26-Myr periodicity of extinctions? (Matters Arising) Nature 321:533.

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6. K.W. Flessa, H.K. Erben, A. Hallam, K.J. Hsü, H.M. Hüssner, D. Jablonski, D.M. Raup, J.J. Sepkoski, Jr., M.E. Soulé, W. Sousa, W. Stinnesbeck, and G.J. Vermeij. 1986. Causes and consequences of extinction. Pp. 235-257. In: D. Jablonski and D.M. Raup, eds. Patterns and Processes in the History of Life (Dahlem Konferenzen 1986). Springer-Verlag; Berlin.

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10. J.J. Sepkoski, Jr. 1987. Periodicity in extinction. AnthroQuest (L.S.B. Leakey Foundation News) No. 37, pp. 19-22.

11. D.M. Raup and J.J. Sepkoski, Jr. 1988. Testing for periodicity of extinction. Science <u>241</u>:94-96.

12. J.J. Sepkoski, Jr. 1988. Alpha, beta, or gamma--where does all the diversity go? Paleobiology <u>14</u>:221-234.

13. A.I. Miller and J.J. Sepkoski, Jr. 1988. Modeling bivalve diversification: the effect of interaction on a macroevolutionary system. Paleobiology <u>14</u>:364-369.

14. J.J. Sepkoski, Jr. 1988. Extinctions of life. Los Alamos Science <u>16</u>:36-49.

15. J.J. Sepkoski, Jr. 1989. Periodicity in extinction and the problem of catastrophism in the history of life. Journal of the Geological Society of London <u>146</u>:7-19.

16. J.J. Sepkoski, Jr. 1990. Evolutionary faunas. Pp. 37-41. In: D.E.G. Briggs and P.R. Crowther, eds. Palaeobiology: A Synthesis. Blackwell; Oxford.

17. J.J. Sepkoski, Jr. 1990. Mass extinction: Periodicity. Pp. 171-179. In: D.E.G. Briggs and P.R. Crowther, eds. Palaeobiology: A Synthesis. Blackwell; Oxford.

<u>Abstracts</u>:

18. J.J. Sepkoski, Jr. and D.M. Raup. 1985. Periodicity in mass extinctions: recent paleontological developments. IGCP 199 meeting, Gwatt, Switzerland.

19. J.J. Sepkoski, Jr. and D.M. Raup. 1985. Periodicity in marine extinction events. EOS 66:813.

20. J.J. Sepkoski, Jr. 1986. The fossil record of evolution: data on diversification and extinction. NASA Conference Publication 2425:103.

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22. A.I. Miller and J.J. Sepkoski, Jr. 1986. Modeling bivalve diversification: the effect of competition on macroevolutionary systems. Geological Society of America Abstracts with Program 18:695.

23. J.J. Sepkoski, Jr. 1987. Periodicity in mass extinction: new data and observations. NASA Space Life Sciences Symposium: Three Decades of Life Science Research in Space. Abstracts, pp. 365-366.

24. J.J. Sepkoski, Jr. 1987. Alpha, beta, or gamma--where does all the diversity go? Geological Society of America Abstracts with Program 19:838.

25. J.J. Sepkoski, Jr. 1988. Patterns of diversity exhibited by the known Proterozoic fossil record. Abstracts for The Proterozoic Biosphere: A Multidisciplinary Study, August 20-22, 1988, PPRG-P, UCLA, Los Angeles. Pp. 57-58.

26. J.J. Sepkoski, Jr. 1988. Periodicity of extinction: a 1988 update. Global Catastrophes in Earth History: An Interdisciplinary Conference on Impacts, Volcanism, and Mass Mortality, Abstract Volume. Lunar and Planetary Institute Contribution No. 673, pp. 170-171.

27. J.J. Sepkoski, Jr. 1989. Extinction events in the fossil record: an overview. Geological Society of America Abstracts with Program 21(4):A47.

28. J.J. Sepkoski, Jr. 1989. The importance of extinction resistance in onshore-offshore changes in faunal dominance during evolutionary radiations. Geological Society of America Abstracts with Program 21(6):A30.

29. J.W. Valentine, B.H. Tiffney, and J.J. Sepkoski, Jr. 1989. The evolutionary dynamics of plants and animals: a comparative approach. Geological Society of America Abstracts with Program 21(6):A146.

I also provided information from the genus-level data base to several colleagues, whose analyses led to publications. These papers are listed below:

30. M. Foote. 1988. Survivorship analysis of Cambrian and Ordovician trilobites. Paleobiology 14:258-271.

31. W.T. Fox. 1987. Harmonic analysis of periodic extinctions. Paleobiology 13:257-271.

32. A. Hallam and A.I. Miller. 1988. Extinction and survival in the Bivalvia. Pp. 121-138. In: G.P. Larwood, ed. Extinction and Survival in the Fossil Record. Clarendon Press; Oxford.

33. D.M. Raup. 1988. Testing the fossil record for evolutionary progress. Pp. 293-317. In: M.H. Nitecki, ed. Evolutionary Ideas of Progress. University of Chicago Press; Chicago.

34. D.M. Raup and G.E. Boyajoian. 1988. Patterns of generic extinction in the fossil record. Paleobiology 14:109-125.

The papers that I authored fall into three general categories:

1. General phenomenology of extinction in the fossil record (publications 6, 7, 8): these investigations used the data base to identify when extinction events occurred, how large they were, and what taxonomic groups were victims or survivors (Fig. 3). I also used the data to examine the environmental distribution of extinctions, demonstrating that nearshore environments promoted comparatively rapid extinction during normal times but suffered no more than offshore environments during mass extinctions.

2. Tests of the 26-myr periodicity of extinction (publications 1, 2, 3, 4, 5, 9, 10, 11, 14, 15, 17): these papers were based upon patterns of generic extinction during the Mesozoic and Cenozoic Eras in the data base. As illustrated in Fig. 4, the new data corroborated the hypothesis of periodicity presented by. Raup and Sepkoski (1984) and provided a more precise picture of the patterns, demonstrating, for example, that several small extinction maxima in the original familial data reflected only small-sample fluctuations and identifying several periodic peaks of extinction not obvious in the older data. In the 1989 version of the genus-level data, all expected positions in the 26-myr series over the last quarter billion years are occupied by local maxima of extinction, and only two additional small peaks of extinction are present. Thus, the hypothesis of periodic extinction remains strong, despite a plethora of published criticisms. Analyses of the data base were used in several instances to answer these criticisms directly (e.g., publications 4, 9, 11, 15).

3. Evolution of diversity among complex organisms (publications 12, 13, 16): these investigations used the data base to examine radiations, rather than mass extinctions, among marine animals. The general approach in these investigations was to

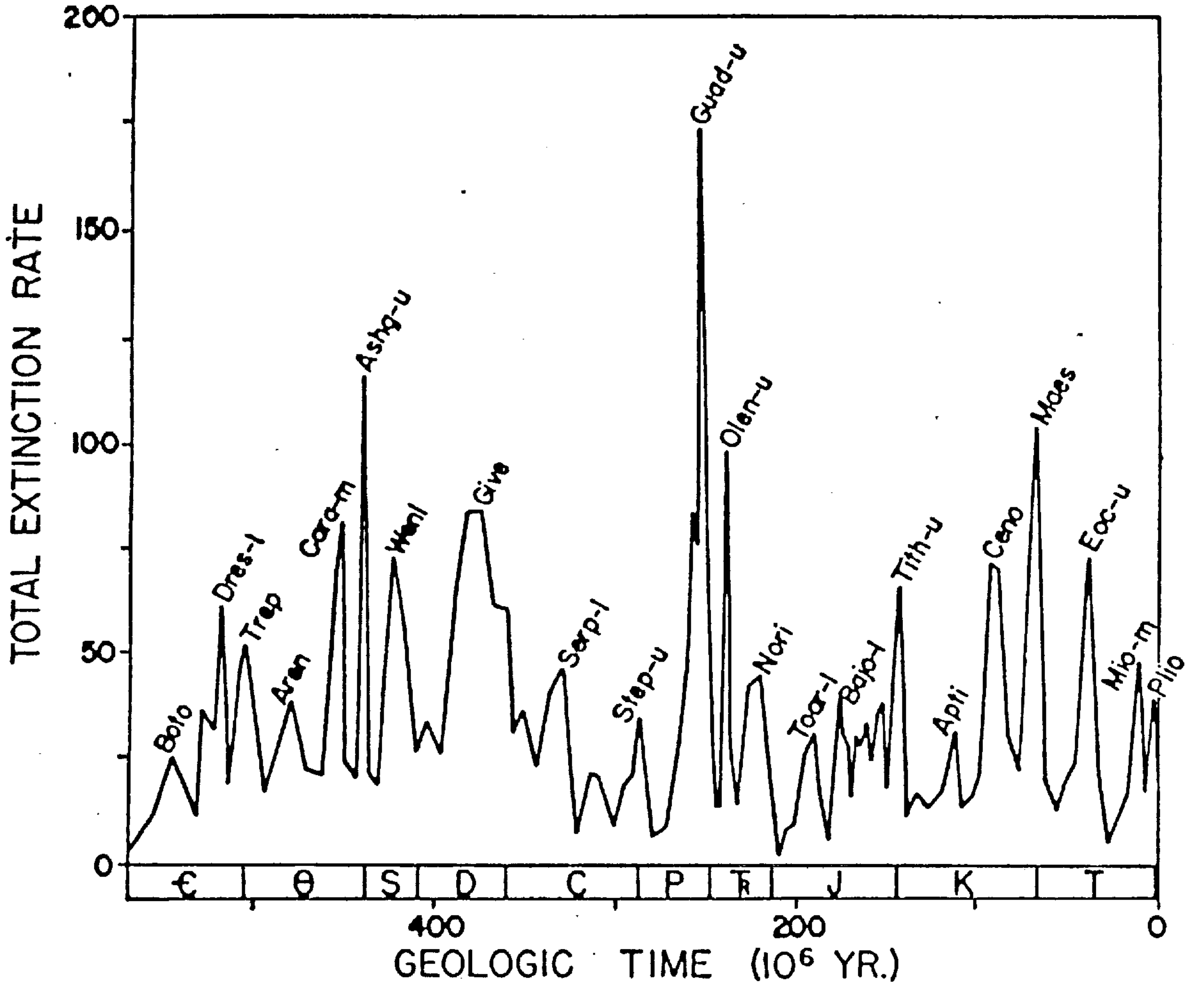

Figure 3. Total extinction rate, in units of extinctions per million years, for marine animal genera over the whole of the Phanerozoic. The time series, computed from the genus-level data base, demonstrates that extinction events (labelled local maxima) are more frequent than previously recognized. Stratigraphic abbreviations over the maxima are as in Fig. 1.

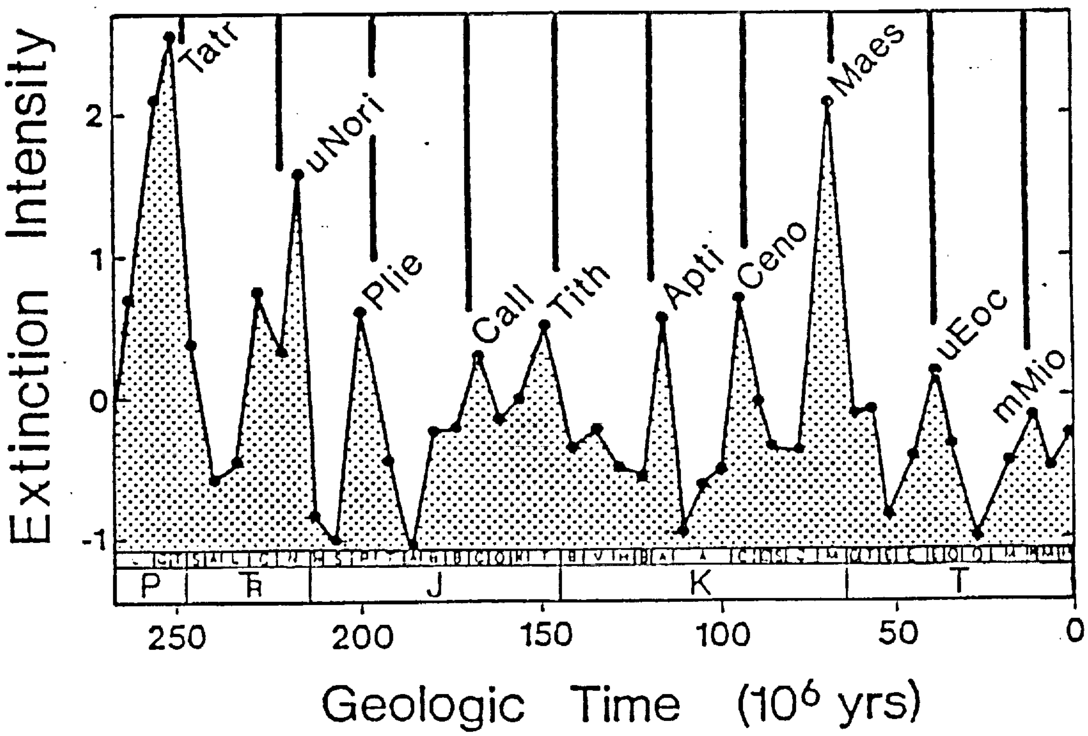

Figure 4. Time series of extinction intensity for marine animal genera from the late Permian to Recent showing the fit of the 26-myr periodic function (vertical lines) to local maxima of extinction. Extinction intensity, compiled from the genus-level data base, was calculated by first computing percent extinction for each of seven major taxonomic groups, then standardizing these time series to equal means and variances, and finally averaging all seven time series. This procedure eliminates bias from certain groups (e.g., ammonoid cephalopods) that have very high turnover rates. Stratigraphic abbreviations over the extinction maxima are as in Fig. 1. (From J.J. Sepkoski, Jr. The taxonomic structure of periodic extinction. In: V. Sharpton and P. Ward, eds. Proceedings of the Conference on Global Catastrophes in Earth History. Geological Society of America Special Publication, in press.)

search for generalities that transcend specific taxa, times, and environments of evolution.

PROSPECTUS

The development of a genus-level data base on the times of origination and extinction of fossil marine animals has provided a valuable resource for studying patterns of extinction and diversification among complex organisms. Investigations to date by myself and colleages have contributed important information on the nature of mass extinction, the timing and regularity of extinction events, and some of the processes and constraints of diversification. These contributions, however, are still incomplete, and much more information should follow as data and analyses become more precise.

The data base remains incomplete and imperfect for many major taxonomic groups and stratigraphic intervals. Data compilation is continuing in effort to rectify these problems. Continued funding under NASA grant NAGW-1693 is permitting further development of the data base, eliminating persisting problems and incorporating the most current information from the international paleontologic literature. It is anticipated that eventually the data base will be of sufficient quality to be published--in both printed and electronic formats--so that it will be accessible to a wide audience of evolutionary scientists. Up to and through that time, I anticipate continuing such analyses that the data base in its current state permits in order to enhance understanding of the nature of extinction, of evolutionary response to perturbation, and of patterns and processes of diversification in marine ecosystems through geologic time.

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